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Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest

Isla H. Myers-Smith,^{1,2} A. David McGuire,³ Jennifer W. Harden,⁴ and F. Stuart Chapin III⁵

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[1] We measured CO₂ and CH₄ exchange from the center of a *Sphagnum*-dominated permafrost collapse, through an aquatic moat, and into a recently burned black spruce forest on the Tanana River floodplain in interior Alaska. In the anomalously dry growing season of 2004, both the collapse and the surrounding burned area were net sinks for CO₂, with a mean daytime net ecosystem exchange of $-1.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while the moat was a CH₄ source with a mean flux of $0.013 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$. Regression analyses identified temperature as the dominant factor affecting intragrowing season variation in CO₂ exchange and soil moisture as the primary control influencing CH₄ emissions. CH₄ emissions during the wettest portion of the growing season were four times higher than during the driest periods. If temperatures continue to warm, peatland vegetation will likely expand with permafrost degradation, resulting in greater carbon accumulation and methane emissions for the landscape as a whole.

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1. Introduction

[2] Carbon stocks in permafrost peatlands, currently protected from fire and decomposition by frozen ground and a high water table, could become significant carbon sources with a change in climate [Turetsky, 2004]. Boreal peatlands contain approximately one quarter of the world's soil carbon (from 260 Pg [Apps *et al.*, 1993] to 270–370 Pg [Turunen *et al.*, 2002] and 455 Pg [Gorham, 1991]) and in low-lying areas, *Sphagnum* peat contains five times the amount of carbon stored in black spruce stands [Trumbore and Harden, 1997]. Cold, waterlogged soils limit decomposition in northern wetlands [Bubier *et al.*, 1998]; however, with coupled warming and drying, these stores of carbon could be released to the atmosphere [Harden *et al.*, 2003; Kasischke and Turetsky, 2006].

[3] Peatlands in the zone of discontinuous permafrost are particularly vulnerable to disturbance [Camill, 2005]. For example, the thawing of ice-rich ground resulting in permafrost collapse, or thermokarst, can transform terrestrial systems to wetlands [Osterkamp *et al.*, 2000; Jorgenson *et al.*, 2001; Davis, 2001]. Permafrost thaw can be initiated by

disturbances such as fire, forest clearing, erosion, flooding and climate warming [Davis, 2001]. Aspect, shading, drainage, and insulation, however, may influence the stability of permafrost even more strongly than changing regional climate change [Camill and Clark, 1998].

[4] In boreal Alaska, roughly 40–60% of the landscape is poorly drained, and characterized by underlying permafrost and shallow water table conditions [Harden *et al.*, 2003]; however, in recent decades permafrost temperatures have been warming. Borehole temperatures around Fairbanks indicate that permafrost temperatures have increase by 1.5°C between the late 1980s and early 1990s [Osterkamp and Romanovsky, 1999]. On the Tanana floodplain, the area of permafrost collapse has increased by 21% since 1949 [Jorgenson *et al.*, 2001]. Loss of permafrost is altering topography, soil moisture and soil thermal properties, resulting in the conversion of lowland forests into wetlands [Jorgenson *et al.*, 2001]. By the end of the century, climate warming may eliminate much of the permafrost in this landscape [Jorgenson *et al.*, 2001].

[5] The timing and magnitude of shifts in temperature and precipitation [Waddington and Roulet, 2000], and the frequency and intensity of regional disturbances such as fire [Kasischke and Turetsky, 2006] and permafrost collapse [Turetsky *et al.*, 2002] interact to determine the seasonal carbon balance in northern peatlands. In order to measure the relative influence of these controls, we investigated carbon exchange along a transect between a fire-scarred, *Picea mariana* forest to a *Sphagnum*-dominated, permafrost collapse. Our results suggest that fire and thermokarst

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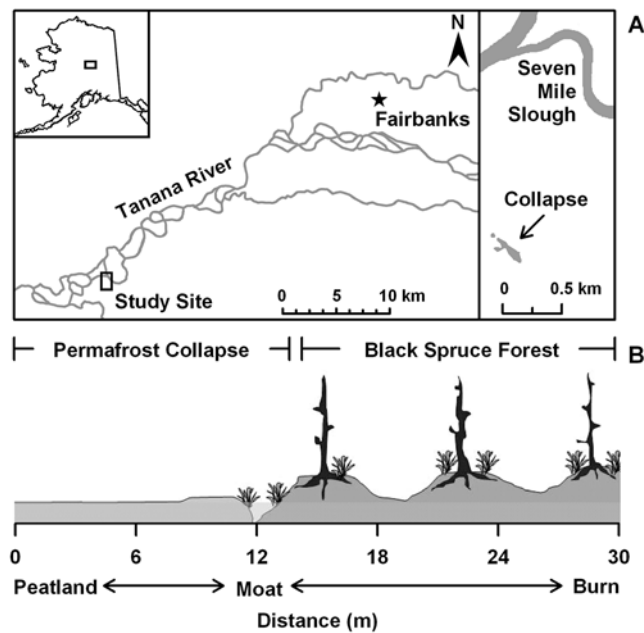


Figure 1. Map of the location of the study site in interior Alaska ($64^{\circ}38.448'N$, $148^{\circ}20.009'W$, 132 m elevation). Diagram illustrating (a) bog and (b) moat (together with the collapse) and burn portions of the transect.

interacted through soil temperature and moisture to control carbon exchange across this landscape.

2. Methods

2.1. Study Site

[6] The permafrost collapse that we studied is located southwest of the Bonanza Creek Experimental Forest on the Tanana River floodplain in interior Alaska ($64^{\circ}N$, 38.448 , $148^{\circ}W$, 20.009 , 132 m elevation; Figure 1). This type of landscape feature occupies approximately 5% of the Tanana

River floodplain [Myers-Smith, 2005]. The study site is isolated from the river flow path as local water level did not correlate significantly with river stage in the 2 years (a) of this study (National Water Information System, USGS; linear regression, inverse transformation, $P = 0.540$). Macrofossil and diatom evidence suggest that the study site has not been part of the active floodplain for at least 600 a [Myers-Smith, 2005]. A transect from the center of a permafrost collapse feature into the surrounding forest was established a month after the Survey Line wildfire burned in June–July 2001. In 2003, two parallel 30-m-long boardwalks were built 5 m apart and 1 m² sample sites were established every 6 m along the eastern boardwalk, creating a transect from the centre of the peatland into the surrounding burned forest.

[7] We identified three vegetation assemblages along the transect: the peatland, moat and the burned black spruce forest. These zones are characterized by distinct hydrologic conditions, vegetation type and disturbance legacy (Figure 1). The peatland is lower in elevation (Figure 2); it has a high water table (Figure 3) and a 0.5-m-thick peat deposit above the mineral soil. In this portion of the transect, dominant vegetation types are *Sphagnum* spp. (primarily *S. riparium* with increased *S. squarrosum* toward the margins of the collapse), *Carex* spp. (primarily *C. canescens*, *C. aquatilis*, and *C. rostrata*), and *Eriophorum angustifolium*. The moat portion of the transect is an area of recent soil collapse. It is dominated by *Eriophorum vaginatum* tussocks, *Carex* spp., and *Eriophorum angustifolium*. Standing water was present in the moat throughout the 2004 growing season. Together the peatland and moat, from 0 to 12 m, comprise the collapse portion of the landscape. The remaining portion of the transect from 12 to 30 m is burned forest.

[8] Before the 2001 fire, the burned portion of the transect was greater than 100-a-old, low-lying, open-canopy black spruce forest with an understory of tussock vegetation. In 2004, most dead trees were still standing. Organic matter depths in the burn are heterogeneous and, the dominant understory vegetation types were *Eriophorum*

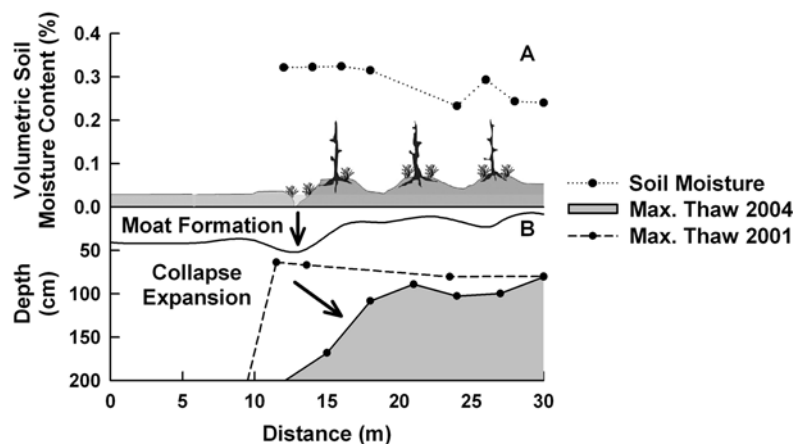


Figure 2. (a) Mean growing season volumetric soil moisture ($n = 2$) and (b) maximum thaw depth in 2001 and 2004 (cm) across the transect. In Figure 2b, the solid line represents the soil surface, the dashed line is the permafrost extent in 2001, and the shaded area is the permafrost extent in 2004.

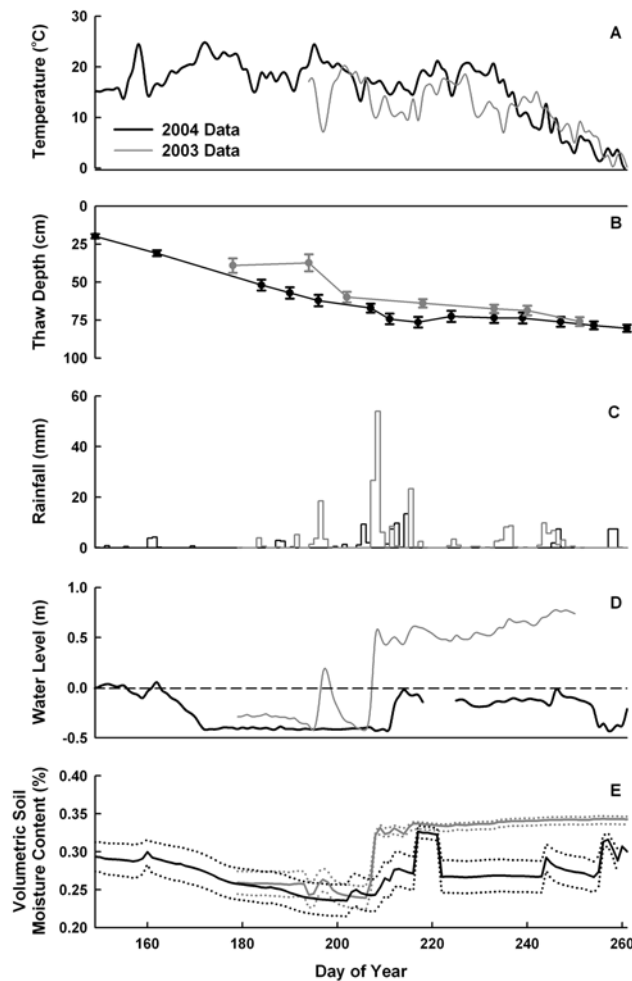


Figure 3. (a) Air temperature, (b) thaw depth, (c) precipitation, (d) water level, and (e) volumetric soil moisture for days 195–250 of 2003 and 2004. The water table depth was measured at 30 m along the transect. Thaw depth and soil moisture data are means (\pm SE, error bars in Figure 3c and dotted lines in Figure 3e) for the burned forest portion of the transect (18–30 m). Thaw and water table depth were measured from the soil surface at the point of measurement.

vaginatum tussocks, *Calamagrostis* spp., *Betula* spp., *Salix* spp., *Potentilla palustris*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*. The vegetation recovered quickly after the burn. By the end of the 2004 growing season, the understory canopy reached over a meter in height, and black spruce seedlings had established.

2.2. Climate

[9] Climate at the study site is typical of interior Alaska. Winters are cold, with mean temperatures below 0°C from October to April. The growing season lasts from early May to mid-September and has three distinct stages: a cool dry period early in May after snowmelt (mean air temperature of 9°C and mean rainfall of 15 mm), a warm dry period in June (mean temperature of 16°C and mean rainfall of 30 mm),

and a cool wet July and August (mean temperature of 14°C and mean rainfall of 50 mm per month) [Viereck et al., 1993] (see also Alaska Climate Research Center, <http://climate.gi.alaska.edu/>). The summer of 2004 was warm and dry with approximately 80 mm of rain (Figure 3), 48% of the climate normal (Alaska Climate Research Center, <http://climate.gi.alaska.edu/>).

2.3. Meteorological Measurements

[10] We installed meteorological instruments at the beginning of the 2003 growing season and logged data at half-hour intervals. We measured soil temperatures using copper-constantan thermocouples (Omega Engineering Inc., Stamford, CT, USA) at 5, 10, 20, and 50 cm depth on both sides of the boardwalk at 0, 10 (west side only) 20, and 30 m distance along the transect. Air temperatures were also measured using copper-constantan thermocouples installed in PVC radiation shields at 30, 60, 120, and 240 cm height above the ground surface. We measured volumetric soil moisture using EC-20 ECH₂O dielectric aquameter probes (Decagon Devices Inc., Pullman, WA, USA) at 16 points along the transect at 12, 14, 16, 18, 24, 26, 28, and 30 m on the both sides of the boardwalk at 10 cm depth. Echo probes were not installed at distances less than 12 m along the transect, because of the influence of *Sphagnum* peat's water holding capacity on soil moisture readings. We measured rainfall using a TE 525MM tipping bucket rain gauge (Texas Electronics Inc., Dallas, TX, USA) installed at 2 m on the tower. To measure soil water table level, we installed a Druck²¹ PDCR 1830-8388 submersible pressure transducer (5 psi range, Druck Inc., New Fairfield, CT, USA) inserted 60 cm below the soil surface, down an 11 cm interior diameter permeable PVC well at 30 m along the transect. We measured photosynthetically active radiation with Apogee quantum sensors (Apogee Instruments Inc., Logan, UT, USA) at 30, 60, 120, and 240 cm above the soil surface. To monitor changes in thaw depth, we pressed a 120 cm or 200 cm fiberglass frost probe into the soil until reaching impenetrable ground. The length of the probe inserted in the soil was considered to be the depth to frozen ground. We conducted three replicate measurements of the active layer every 3 m along both sides of the transect at each visit to the site (every one to two weeks throughout the growing season).

2.4. Fluxes

[11] We measured CO_2 and CH_4 fluxes using a closed chamber system. Flux measurements were conducted during daylight hours every one to two weeks, resulting in 16 CO_2 and 13 CH_4 flux measurements throughout the growing season of 2004. We measured fluxes at permanent plots established from the center of the peatland into the surrounding burn and conducted two replicate measurements taken at 0, 6, 12, 18, 24, and 30 m on both sides of the transect.

[12] We measured CO_2 fluxes using a Li-840 infrared gas analyzer (Licor Inc., Lincoln, NE, USA). The chamber was connected to the IRGA using flexible tubing in a closed circuit, and a miniature pump (GAST, Benton Harbor, MI) produced gas flow through the analyzer and back to the chamber at a rate of 0.5 L min^{-1} . We conducted CO_2 flux measurements for 2 min with data logged to a laptop

computer at a 0.5 second interval. Fluxes were calculated using the first half minute of data, discarding the first few seconds of measurement, which minimized any influence of changing chamber temperature over the course of the measurement. Because the chamber was large and had very small chamber vents as per Davidson *et al.* [2002], we assumed pressure effects to be minimal lasting only over the first few seconds of the measurement. To account for measurement variability, we conducted two measurements in succession at each location, after flushing the chamber for accumulated CO₂.

[13] We constructed chambers of 61 × 61 cm square, with a height of 30.5, 61, or 122 cm, large enough to encompass the vegetation, yet small enough to be portable. We used the shorter chambers in the collapse portion of the transect, where the canopy of the vegetation was shorter. Chambers included a fan for air circulation, inlet and outlet ports for CO₂ measurements, or just outlet ports for CH₄ measurements [Carroll and Crill, 1997]. We placed chambers directly on the soil surface in marked plots. The chamber base was wrapped in closed-pore foam pipe insulation and plastic sheeting fastened to the chamber base was weighed down around the plot to make a solid seal with the soil surface.

[14] We conducted measurements of both net ecosystem exchange (NEE) and ecosystem respiration (ER) on each plot by measuring CO₂ flux in full light and in darkened chambers. To quantify CO₂ derived from soil and plant respiration (ecosystem respiration, ER) we used a two-layer cloth shroud with a reflective surface to exclude solar radiation. NEE data are not reported as NEE_{max} (NEE at PAR > 1000 μmol m⁻² s⁻¹) as PAR only once surpassed 1000 μmol m⁻² s⁻¹ during field measurement trips in 2004.

[15] We conducted 40 min methane flux measurements to compensate for low flux rates and large chambers. Gas samples were collected and stored in 20 mL BD Luer-Lok™ syringes (Becton, Dickinson and Company, Franklin Lakes, NJ, USA). Syringe samples were taken after deploying the chamber and at 8 min intervals, yielding six gas samples. We analyzed samples within 48 h of collection using a Varian CP-3800 gas chromatograph with a flame ionization detector (Varian Inc., Palo Alto, CA, USA), which was calibrated before each use using standard gases (CH₄: 99.9 and 1020 ppb).

[16] We calculated CO₂ and CH₄ flux rates using linear regressions of gas concentrations over time. We excluded all data sets that did not exhibit initial linear changes in concentration ($R^2 < 0.9$), this resulted in the omission of 3% of NEE and ER measurements and 4% methane flux measurements. The minimum detection limit for fluxes were 0.1 μmol CO₂ m⁻² s⁻¹ for CO₂ and 0.002 μmol CH₄ m⁻² s⁻¹ for CH₄. Fluxes that did not increase above or below the minimum detection limit were considered to have a rate of 0.

2.5. Biomass

[17] We established a second 30-m transect from the collapse into the surrounding lowland burn, 30 m to the east of the intensively monitored transect, and established plots from the center of the peatland into the surrounding burn at 0, 6, 12, 18, 24, and 30 m on the east and west side of the new transect. At each plot, we harvested a 61 × 61 cm

area (consistent with the size of the chamber plots) for aboveground biomass at the end of the growing season (DOY 231) in 2004 and sorted these aboveground biomass samples by major species or species groups. For the *Sphagnum* moss, we classified only green-colored tissues as aboveground biomass. Photosynthetic green tissues were separated from the aboveground biomass samples. Samples were dried at 60°C to measure the dry mass. Samples were also analyzed for % C and % N.

[18] We calculated the percent cover of vegetation for the destructively harvested biomass transect and the intensively monitored study transect (where flux measurements were taken) from digital photographs. Photographs were rectified to 10,000 × 10,000 pixels and a 20 × 20 grid was applied to the photograph. The percentage of each plant type was estimated in each grid cell. We then regressed the percent cover against the measured dry biomass for the biomass transect data to project biomass for the intensively measured transect. We did not project moss biomass and instead assumed it to be the same for both transects.

[19] We projected the change in biomass over the growing season from the change in greenness determined from digital photographs. We chose five dates throughout the growing season with pictures of equal color saturation, focus and aspect. From these we estimated the percent photosynthetic biomass by calculating the percent of green areas as a proportion of the total pixels of the photograph. We fit curves for the change in percent green versus time for 0, 6 m and the mean of the remaining distances along the transect (12, 18, 24, and 30 m), as these two regions of the transect exhibited different patterns of greenness across the growing season of 2004. To estimate photosynthetic biomass over the growing season, we used these relationships to correct the biomass estimates for the intensively monitored transect to account for the change in percent of green vegetation associated with growth and senescence.

2.6. Soils

[20] We collected frozen soil cores using a gasoline-powered corer in March 2003, taking 2 to 4 cores every 3 m along the transect, yielding a total of 35 cores. The 35 cores were stored frozen until partitioning into different soil layers using a radial saw. We classified soils using the Canadian Soil Classification system [Soil Classification Working Group, 1998] identifying fibric, mesic, and humic organic horizons and the A and C mineral horizons. We sampled 26 cores into the A or C horizons of the mineral soil (core depths ranging between 7 and 80 cm). Nine cores were sampled only to the mineral boundary (core depths ranging between 2 and 68 cm). We measured bulk density, % C and % N for all soil samples.

2.7. Carbon and Nitrogen Analysis

[21] We oven dried at 50°C–65°C all soil and plant samples before analysis. Samples were ground in a tumbling ball mill for 2–5 min until homogenized into a powder. We analyzed samples for percent C and percent N using a Carlo Erba EA1108 CHNS analyzer (CE Instruments, Milan, Italy) and a COSTECH ECS 4010 CHNS-O analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). Sample standard errors were ±0.01% for nitrogen, ±0.45% for carbon. For the biomass transect samples,

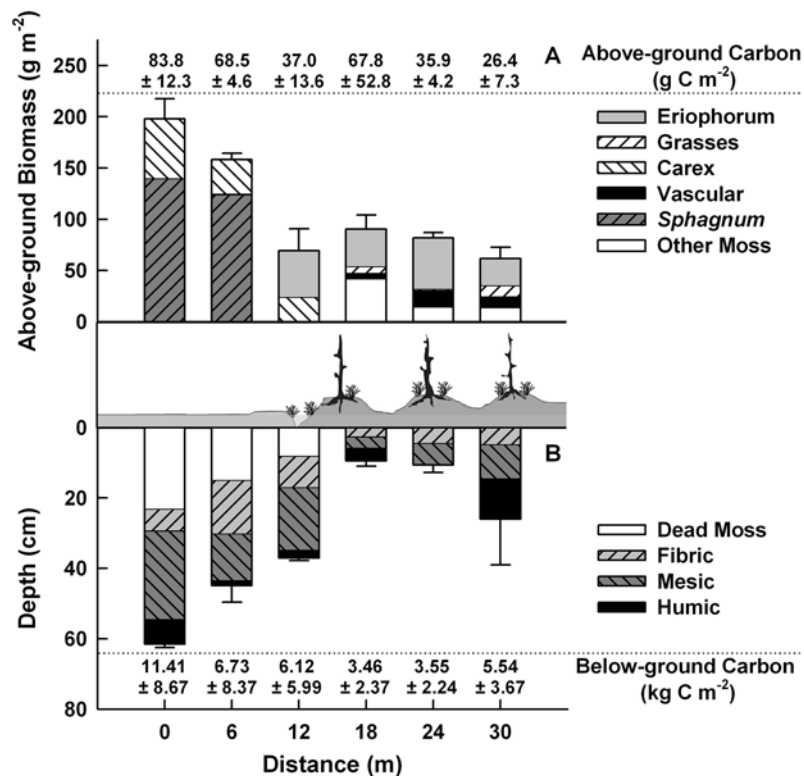


Figure 4. (a) Mean above-ground biomass (g m^{-2} , $n = 2$) and (b) mean measured soil horizon depths (cm, $n = 2$) described using the Canadian Soil Classification system [Soil Classification Working Group, 1998]. Summary numbers above and below bars indicate the mean above-ground carbon (g m^{-2} , $n = 2 \pm \text{SE}$) for the total biomass and the mean below-ground carbon (kg m^{-2} , $n = 3 \pm \text{SE}$) for all organic soil horizons at each distance along the transect.

we analyzed for percent C and percent N when the samples were more than 10% of the plot biomass allowing for representative sampling of carbon and nitrogen from the dominant plant types.

2.8. Statistical Analysis

[22] We performed all statistical analyses in SPSS 10.0 (SPSS Inc., Chicago, IL, USA) and in JMP IN 5.1.2 (SAS Institute Inc., Cary, NC, USA). We used multiple linear regression models to relate C gas fluxes to six explanatory variables (predictors): soil temperature (at 5 cm depth), thaw depth, PAR, green biomass, soil moisture (at 10 cm depth), and water table depth. These variables are known to influence carbon exchange in peatlands [Blodau, 2002; Hobbie et al., 2000; Gorham, 1991]. Before analysis, we transformed (e^x) the soil temperature data to meet assumptions of normality and equal variance. Smoke from wildfires through July and August reduced PAR during the growing season of 2004, and as a result, few flux measurements were conducted at high light intensities. We did not observe a saturating relationship with PAR for the entire bog or burn data sets (at 12 and 18 m along the transect significant logarithmic relationships were observed); therefore we used linear rather than hyperbolic regression to model the controls over NEE. We assumed that multicollinearity was minimal in these data because tolerance ($1 - R^2$ of each variable regressed upon the others) exceeded 0.5 for all

explanatory variables. Simple linear regressions for each parameter are also presented for comparison. The difference between the significance of the multiple linear regressions and the sum of the significance for the simple linear regressions for each parameter is less than 0.15 for all models. This suggests that colinearity between parameters is minimally altering the significance of the multiple linear regression models. We developed separate empirical models for the collapse and burn portions of the landscape. The peatland and moat portions of the transect were combined for the empirical modeling analysis because sample size was limited in the moat (2 sample points). The ratio of dependent data points to independent variables ranged from 42:6 to 51:6 across the models that we developed.

2.9. Data Reporting

[23] Field and analytical data are reported for all sites and samples at <http://www.lter.uaf.edu/> listed under the investigator Isla Myers-Smith. Archive samples are stored at U.S. Geological Survey at Menlo Park.

3. Results

[24] Above and belowground carbon stores varied across the transect. The carbon stored in live, aboveground vegetation was highest in the center of peatland and lowest at 30 m in the burned portion of the transect (Figure 4). The

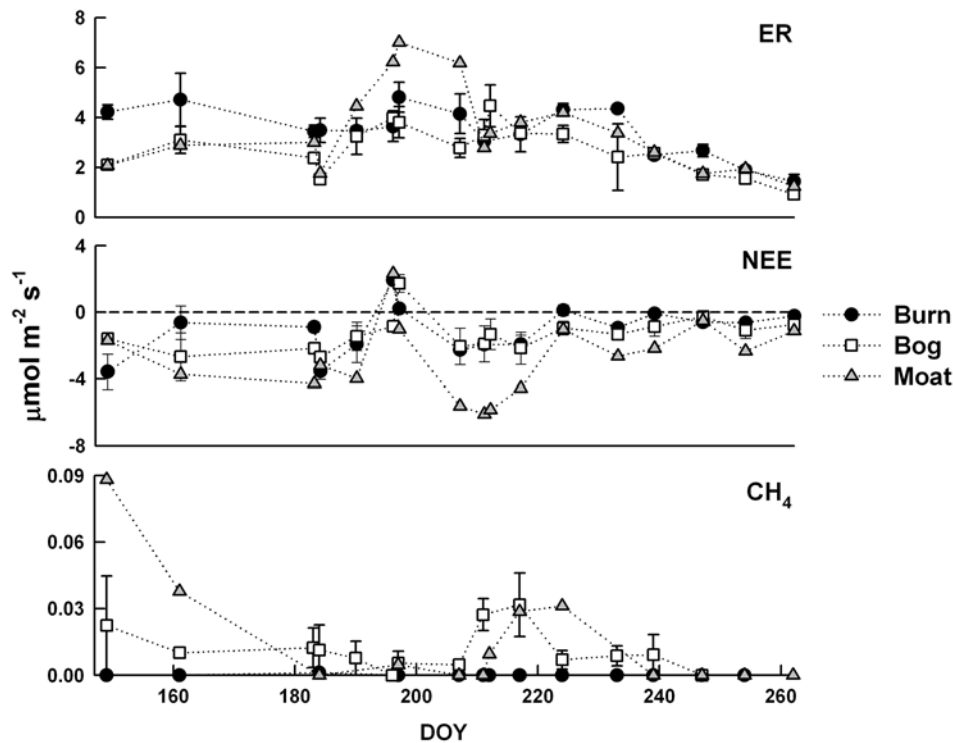


Figure 5. Mean ER, NEE, and CH_4 fluxes for the across the transect for the growing season of 2004 ($n = 2$, bog; 1, moat; 3, burn; error bars are $\pm\text{SE}$). Carbon uptake is denoted with negative numbers, and carbon emissions are denoted with with positive numbers. NEE data are midday measurements representing a range in PAR of $77\text{--}1411 \mu\text{mol m}^{-2} \text{s}^{-1}$.

organic horizon was thicker and organic carbon storage greater in the collapse portion of the landscape (Figure 4). The greatest organic soil carbon storage of 11 kg C m^{-2} occurred at the center of the peatland where the humic layer was thickest ($61.5 \pm 3.5 \text{ cm}$) along the transect.

[25] Carbon exchange was highly variable across the growing season, with differing patterns of fluxes over time for each of the different landscape units: burn, moat and peatland (Figure 5). For all sites along the transect, the mean growing season ER was $3.2 \pm 0.30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ($n = 6$, $\pm\text{standard error (SE)}$), and daytime NEE was $-1.4 \pm 0.38 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ($n = 6$, $\pm\text{SE}$) in 2004 (Figure 5). Methane fluxes in the burn were below measurement detection (less than $0.002 \mu\text{mol CH}_4 \text{ m}^{-2} \text{s}^{-1}$). The mean growing season CH_4 flux in the collapse portion of the transect was $0.013 \pm 0.002 \mu\text{mol CH}_4 \text{ m}^{-2} \text{s}^{-1}$ ($n = 6$, $\pm\text{SE}$). We observed the highest variation in fluxes across the growing season in the moat (coefficient of variation, CO_2 respiration = -0.79 , NEE = 0.49 , and CH_4 = 1.68).

[26] CO_2 and CH_4 fluxes differed in their patterns of variation along the transect (Figure 6). Ecosystem respiration was lowest in the peatland in comparison with the moat and burn. Net ecosystem exchange was most negative in the moat, indicating higher daytime rates of carbon uptake than at other points along the transect. Methane flux was highest in the moat and peatland center, where soil moisture was highest.

[27] Effects of temperature and moisture on fluxes were compared by averaging the upper and lower 10th percentiles

of the measurements. For these periods of extremes of temperature and moisture, variation in fluxes were significant (at least $p < 0.1$) for all landscape units with the exception of ER in the burn and NEE in the collapse between the dry and wet extremes, and CH_4 in the collapse between hot and cold extremes (Figure 7).

[28] Multiple linear regression models (Table 1) for carbon exchange suggested that flux varied significantly with landscape unit (Figure 8). Soil temperature was the main variable influencing ER in the collapse, and moisture was an additional important control in the burn. Net ecosystem exchange was primarily influenced by soil temperature (Table 1) in burn and the collapse, although these models explain less than 33% and 19% of the variation in observed fluxes, respectively, in the burn and the collapse. The dominant control on methane fluxes in the collapse was soil moisture, with biomass also explaining significant variability. We were not able to estimate the growing season carbon balance, because these models of carbon exchange did not explain enough of the variation over time.

4. Discussion

[29] Fire and thermokarst interacted to alter carbon exchange across the transect from the *Sphagnum*-dominated permafrost collapse, through the aquatic moat, and into the recently burned black spruce forest. In the burned forest, fire reduced organic matter thickness, increased summer albedo and changed vegetation composition, which in turn

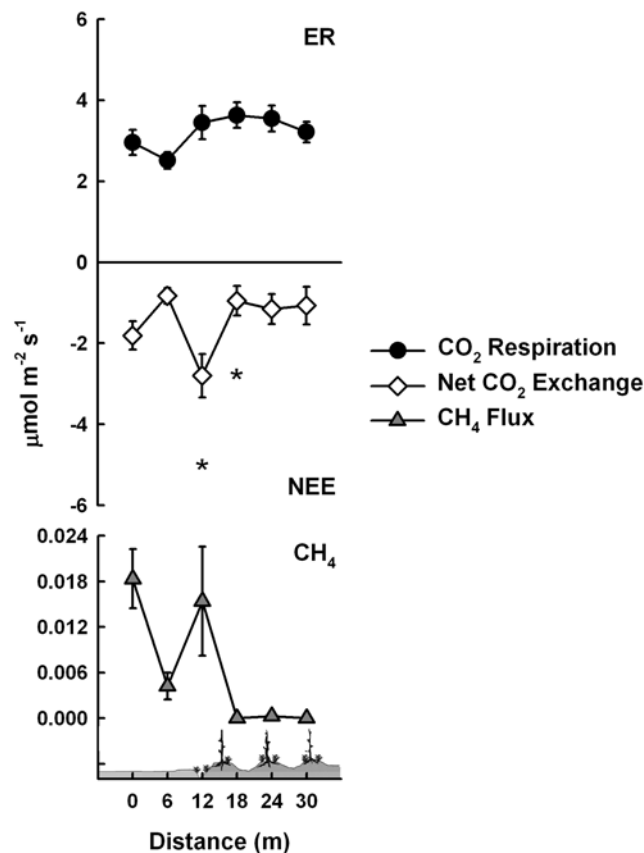


Figure 6. Mean ER, NEE, and CH₄ fluxes across the transect for the growing season of 2004 (error bars are \pm SE; n (sample days) = 16 for CO₂ and NEE and n = 13 for CH₄). Carbon uptake is denoted with negative numbers, and carbon emissions are denoted with positive numbers. NEE data represent the mean of midday measurements representing a range in PAR of 77–1411 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Asterisks denote NEE_{max} (NEE at 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for sites along the transect that exhibited a significant relationship between PAR and NEE (logarithmic regression 12 m, $F_{1,15} = 4.43$, $P = 0.053$; 18 m, $F_{1,15} = 4.65$, $P = 0.048$).

influenced the soil temperature, thaw depth, and soil moisture. In the moat, collapse caused aerobic soils to become saturated, changing the ratio of oxic to anoxic decomposition. In the peatland, carbon in the peat was protected by a high water table; although, reduced precipitation in the summer of 2004 exposed carbon stocks to aerobic decomposition.

[30] Temperature was the dominant control of within-growing season variation in CO₂ exchange in both the collapse and burn (Figure 8); however, both CO₂ and CH₄ fluxes were affected by moisture availability. In comparison to the wettest points of the summer, the driest times were characterized by lower net uptake of CO₂ in the burn and lower methane fluxes in the collapse (Figure 7). May–September rainfall for 2004 was in the 20th percentile of the frequency distribution (48% of normal) for precipitation data collected since 1909 (Alaska Climate Research Center, <http://climate.gi.alaska.edu/>). Low albedo, loss of organic

matter and reduced moss cover interacted with the warm and dry growing season to reduce soil moisture in the burn, with patches of dry soil occurring even when the water table was less than half a meter below the soil surface. These dry conditions limited plant activity and decomposition, resulting in reduced carbon exchange.

[31] The peatland portion of the landscape acted as a net C sink, accumulating organic matter that was protected from aerobic decomposition by a high water table. The lowest observed carbon exchange occurred at 6 m in the peatland portion of the transect, where a hummock reduced soil moisture at the peat surface. In the driest time of the summer, we attribute lower net uptake of CO₂ in the burn to moisture limitation of photosynthesis. Methane fluxes measured in the collapse during the growing season of 2004 ($0.013 \pm 0.002 \mu\text{mol CH}_4 \text{m}^{-2} \text{s}^{-1}$) were low relative to fluxes measured in other northern peatlands (Table 2). An application of the empirical model we developed indicates that methane emissions would have been three times greater given meteorological conditions experienced during the growing season of 2003.

[32] Fluxes were most variable in the moat during the 2004 growing season. In this portion of the transect, variable water levels, active thermokarst and deep thaw promoted both aerobic and anaerobic decomposition. Because of the high biomass of *Eriophorum vaginatum*, ER was more than offset by carbon uptake, resulting in strongly negative NEE. In addition to high rates of ER and NEE, methane release was elevated in the moat. Previous studies have also documented high methane emissions at the margins of collapse features [Liblik *et al.*, 1997; Turetsky *et al.*, 2002; Christensen *et al.*, 2004; Bubier *et al.*, 2005]. These higher methane emissions could be attributed to more anaerobic soils, vegetation mediated methane release [Bellisario *et al.*, 1999] or input of labile carbon from the surrounding catchment [Koprivnjak and Moore, 1992].

[33] Plant community composition varied along the transect from the *Sphagnum*-dominated peatland to the vascular vegetation of the burn. Vascular biomass explained 46% of the variation in the mean growing season ER for all plots across the transect (linear regression, $P = 0.02$). Since the plant community covaried with moisture, active layer depth and topography, the relative contributions to ER of abiotic parameters such as soil temperature and moisture could not be completely isolated from biotic parameters such as plant activity and litter quality. The relationship between estimated litter decomposition (based on mean k values for moss = 0.03, sedge = 0.2, and other vascular plants = 0.1 [Hobbie, 1996]) and mean growing season ER for all flux plots across the transect was not significant (linear regression, $R^2 = 0.22$, $P = 0.12$).

[34] Loss of dissolved organic carbon is an important component of the carbon balance in northern peatlands [Moore *et al.*, 1998; Waddington and Roulet, 2000; Fraser *et al.*, 2001]. We did not account for DOC loss or transfers in this study; however, because our study site is contained in a closed drainage basin no loss of DOC should occur from the system as a whole. In addition, the hummock-hollow topography of the burned landscape (Figure 2) and shallow active layer likely prevented much lateral water flow from the surrounding area into the collapse.

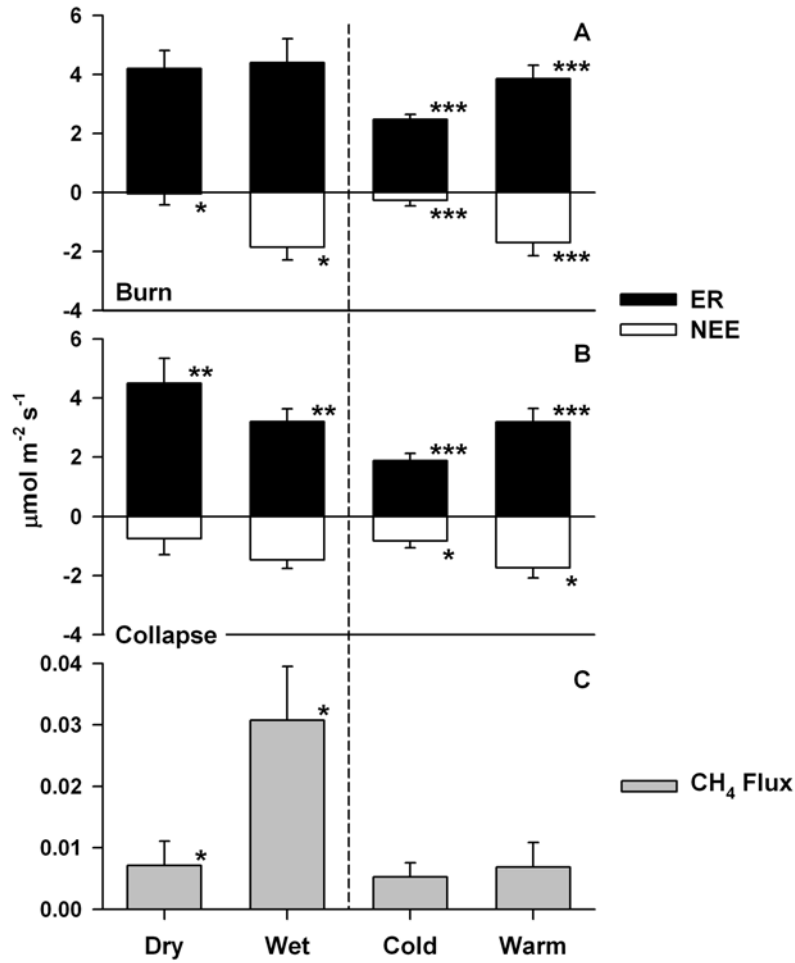


Figure 7. Mean ER and NEE fluxes for the (a) burn and (b) collapse and (c) CH₄ fluxes in the collapse for the 10th percentile of the frequency distribution of the driest, wettest, coldest, and warmest flux measurements of the growing season of 2004 (error bars are \pm SE, $n = 4\text{--}11$). Asterisks denote significance (three asterisks, $P \leq 0.01$; two asterisks, $P \leq 0.05$; one asterisk, $P \leq 0.1$). Analysis of variance for soil moisture is as follows: collapse ER, $F_{1,18} = 5.04$, $P = 0.03$; collapse NEE, not significant (ns); collapse CH₄, $F_{1,13} = 4.39$, $P = 0.06$; burn ER, ns; burn NEE, $F_{1,14} = 3.30$, $P = 0.09$). Air temperature is as follows: collapse ER, $F_{1,12} = 11.20$, $P = 0.01$; collapse NEE, $F_{1,12} = 3.57$, $P = 0.08$; collapse CH₄, ns; burn ER, $F_{1,12} = 8.48$, $P = 0.01$; burn NEE, $F_{1,12} = 8.48$, $P = 0.01$.

Table 1. Model R^2 , Significance, Degrees of Freedom, and Unstandardized b Coefficients for Multiple Linear Regression Models of CO_2 and CH_4 Fluxes for the Collapse (0–12 m) and Burn (18–30 m) Portions of the Transect^a

	Multiple Linear Regressions														
	Ecosystem Respiration						Net Ecosystem Exchange						CH_4 Flux		
	Collapse			Burn			Collapse			Burn			Collapse		
R^2	0.49			0.56			0.19			0.33			0.35		
Significance	<0.01			<0.01			0.05			<0.01			0.01		
DF	3,47			4,43			2,48			3,44			3,37		
b coefficients \pm SE															
Constant	1.3 \pm 0.4			−1.8 \pm 2.2			−1.7 \pm 0.5			−2.3 \pm 0.6			−0.12 \pm 0.04		
Soil temperature	3.2e ^{−6} \pm <0.1			2.1e ^{−6} \pm <0.0			2.3e ^{−6} \pm <0.1			3.1e ^{−6} \pm <0.1			ns		
Soil moisture	ns			18.6 \pm 7.2			ns			ns			0.45 \pm 0.1		
Water level	ns			ns			ns			ns			ns		
Thaw depth	ns			−2.6e ^{−2} \pm <0.1			ns			2.2e ^{−2} \pm <0.1			−7.0e ^{−6} \pm <0.1		
PAR	1.1e ^{−3} \pm <0.1			ns			−1.5e ^{−3} \pm <0.1			ns			ns		
Biomass	4.9e ^{−3} \pm <0.1			8.9e ^{−3} \pm <0.1			ns			−7.5e ^{−3} \pm <0.1			1.1e ^{−4} \pm <0.1		
Linear Regressions (for each parameter)															
	R^2	Sig.	DF	R^2	Sig.	DF	R^2	Sig.	DF	R^2	Sig.	DF	R^2	Sig.	DF
Soil temperature	0.39	<0.01	1,49	0.16	<0.01	1,46	0.14	0.01	1,48	0.21	<0.01	1,46	ns	ns	ns
Soil moisture	0.12	0.01	1,49	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.17	<0.01	1,39
Water level	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.07	0.11	1,39
Thaw depth	ns	ns	ns	0.16	0.01	1,46	ns	ns	ns	0.08	0.05	1,46	ns	ns	ns
PAR	ns	ns	ns	0.07	0.08	1,46	0.08	0.05	1,49	ns	ns	ns	ns	ns	ns
Biomass	0.11	0.02	1,49	0.16	<0.01	1,46	ns	ns	ns	ns	ns	ns	ns	ns	ns

^aTemperature data were exponentially transformed before analysis. Parameters were removed from multiple linear regression models if significance >0.5. All simple linear regression models with significance >0.1 are denoted as not significant (ns).

[35] The relative abundance of different patch types in the landscape is changing because of fire and thermokarst; therefore projections of ecosystem feedbacks to climate change in relation to weather variables alone may be incorrect. Despite the fact that there is great uncertainty about the future precipitation regime [Rouse *et al.*, 1997], climate models indicate that much of the boreal region will experience warmer temperatures and reduced soil moisture

[Roulet *et al.*, 1992; Wrona *et al.*, 2004]. A warmer climate will alter carbon emissions in northern wetlands both directly, and indirectly thorough changes in permafrost integrity, and associated changes in hydrology and vegetation [Christensen *et al.*, 2004]. Both carbon accumulation and methane emissions have been shown to increase with permafrost degradation in peatlands of western Canada [Robinson and Moore, 2000; Turetsky *et al.*, 2000; Vitt *et*

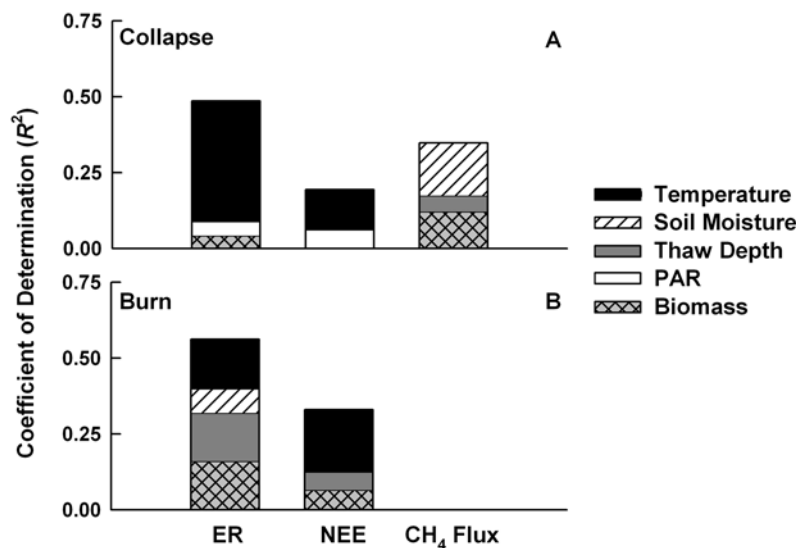


Figure 8. Proportion of variation explained by each significant model parameter for multiple linear regression models of all fluxes for the (a) burn and (b) collapse portions of the landscape. All models are significant at $P < 0.05$.

Table 2. Midpoint of the Range of Methane Fluxes for Studies of Boreal Permafrost Peatlands^a

Study	Location	Midpoint of the Range in Reported CH ₄ Flux, $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$
Moore and Knowles [1987]	Schefferville, Northern Québec	0.04
Moosavi et al. [1996]	near Fairbanks, Alaska	0.51
Liblik et al. [1997]	Fort Simpson, North West Territories	0.10
Bubier et al. [1995]	near Thompson, Manitoba	0.04
Panikov and Dedysh [2000]	western Siberia	0.22
Alm et al. [1999]	eastern Finland (dry year)	0.042
Waddington and Roulet [2000]	near Umeå, Northern Sweden	−0.037
Heikkinen et al. [2002]	northern Finland	0.14
Turetsky et al. [2002]	north central Saskatchewan	0.0019
Huttunen et al. [2003]	northern Finland	0.27
Christensen et al. [2004]	Åbisko, Northern Sweden	0.049
G. J. Whiting (personal communication, 2005)	northern Alberta	0.10

^aThe mean, median, range, and midpoint of the range for our data are 0.012, 0.0051, 0–0.088, and 0.044 $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$.

al., 2000; Camill et al., 2001; Bubier et al., 1995]. At our study site, peatland vegetation will likely expand into the moat. Soil profiles along the transect and measured growing season fluxes indicate that further increases in the collapse will increase carbon accumulation and methane emissions for the landscape as a whole; however, a drier climate or the initiation of subsurface drainage could cause a release of soil carbon stores through decomposition or fire. To better understand this heterogeneous landscape, future research should focus on mapping permafrost degradation and measuring the impacts of wetland formation and drainage on the fire regime and carbon balance of interior Alaska.

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